

MACRO-HABITAT FEATURES ASSOCIATED WITH PAINTED AND INDIGO BUNTINGS IN NORTHEAST TEXAS

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ABSTRACT.—Habitat features found within 4.1 ha sample areas surrounding the song perches of 33 Indigo Buntings (*Passerina cyanea*) and 33 Painted Buntings (*Passerina ciris*) in northeast Texas were compared to determine whether these species segregated according to habitat. The species did not differ in the proportions of open habitat or the type and amounts of successional and mature woodland in the sample areas surrounding their song perches. Indigo Buntings were mostly associated with lower elevations where they occurred along the edges of successional and mature woodlands. Painted Buntings showed no elevation bias. Compared to Indigo Buntings, Painted Buntings were associated with smaller, more numerous, and more heterogeneous stands of trees. In general, Indigo Buntings typically occurred where there were open areas within otherwise wooded habitats whereas Painted Buntings tended to occur where there were wooded areas in otherwise open habitat. Received 17 June 1999, accepted 28 Sept. 1999.

Indigo Buntings (*Passerina cyanea*) are a familiar passerine that breed through much of North America east of the Great Plains. In central and west Texas, they are largely replaced by the congeneric Painted Bunting (*Passerina ciris*; Sauer et al. 1997). However, there is a broad zone of overlap between these two species extending across much of Oklahoma, east Texas, and Louisiana where both are equally abundant (Sauer et al. 1997).

The habitats of both Indigo and Painted buntings are described in the popular literature as brushy areas, river and streamside thickets, and forest edges (Peterson 1947, Robbins et al. 1983). However, Parmelee (1959) observed that Painted and Indigo buntings were seldom observed in the same areas in Oklahoma. This suggests that, at least where these buntings are sympatric, the two species might occupy different habitats.

Taber and Johnston (1968) provided a qualitative overview of the habitats frequented by Indigo Buntings, but there are no studies quantifying the habitats of this species (Payne 1992). However, Indigo Buntings appear in a number of studies on avian community associations relative to habitat features (Posey 1974, Conner et al. 1983, Yahner 1986, Best et al. 1995), ecological gradients (Johnston and Odum 1956, Shugart and James 1973), and habitat alteration (Stauffer and Best 1980, Strelke and Dickson 1980, Triquet et al. 1980,

Yahner 1993). Thus, albeit indirectly, the breeding habitat of the Indigo Bunting has been well documented through many portions of its geographic distribution. On the other hand, there is little quantitative data on habitat features associated with Painted Buntings (Lowther et al. 1999). A single quantitative study of Painted Bunting breeding habitat was conducted at the northern edge of the species' distribution in Missouri (Norris and Elder 1982). In addition, there are three qualitative descriptions: one by Parmelee (1959), a second by Sprunt (1968), and a third by Lowther and coworkers (1999). Painted Bunting habitats are cursorily identified in three avian community studies; two in southeast Texas (Dickson and Segelquist 1979, Dickson et al. 1995) and one near the periphery of the species' distribution in northwest Arkansas (Shugart and James 1973). There is no information on whether sympatric populations of Indigo and Painted buntings are ecologically segregated relative to habitat.

The objective of our study was to provide a quantitative description of Indigo and Painted bunting habitat in northeast Texas by evaluating macro-habitat features around the song perches of territorial males and to test the hypothesis that, in northeast Texas, Indigo and Painted buntings are segregated according to habitat.

METHODS

Study area.—The study was conducted on the agricultural property of Texas A&M University–Commerce adjacent to the city of Commerce (33° 15' N, 95° 55' E) in Hunt Co., Texas. The study area consisted

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of 5.5 km² of land that varied considerably in elevation and habitat types, but which reflected variation typical of this region. About 60% of the area consisted of managed and unmanaged pasture interspersed with wooded streambanks, bottomland woods, upland woods, and fencerows. The woody vegetation in these pastures varied considerably and contained a wide variety of secondary and mature growth. Cropland, active and idle, accounted for about 15% of the area. These fields contained no woody vegetation but were often bordered by shrubby fencerows. About 10% of the area was managed and unmanaged hay fields. These areas were bounded by shrubby fencerows and, in one case, contained a streamside thicket and isolated stands of trees. The rest of the study area was bottomland woods and idle land in various stages of succession. Dominant trees on the study area were black oak (*Quercus velutina*), hickory (*Carya* spp.), green ash (*Fraxinus pennsylvanica*), sugarberry hackberry (*Celtis laevigata*), pecan (*Carya illinoensis*), cedar elm (*Ulmus crassifolia*), osage orange (*Maclura pomifera*), honey locust (*Gleditsia triacanthos*), post oak (*Quercus stellata*), red cedar (*Juniperus virginiana*), plum (*Prunus* spp.), and persimmon (*Diospyros virginiana*).

The topography varied from level to slightly rolling. Several drainages ran through the area with intermittent creeks on upland sites and permanent creeks in bottomland areas. A small river, the South Sulphur River, ran through the middle of the study area. In addition, several stock ponds were distributed throughout. Drainages were typically lined with scrubby trees in upland sites and larger, thicker woods in bottomland areas. Mature bottomland woods grew along the South Sulphur River.

Data collection and analyses.—Song perches were located between 06:00 and 12:00 from 5 May 1996 through 25 June 1996 and were plotted onto maps of the study area. The song perches used for analysis were always the first perch from which an individual was observed singing. Subsequently, we used spot-mapping (Robbins 1970) to discriminate the owners of the perches and to verify that adjacent song perches represented different individuals. Spot mapping can cause some individuals to be overlooked while others are duplicated (see review in Verner 1985). We were most concerned with the latter type of error and took measures to eliminate the duplication of individuals in the sample. When a song perch was identified, we also plotted the locations of immediate neighbors. These simultaneous registrations (Robbins 1970) ensured that adjacent song perches did not belong to the same individuals. Furthermore, Painted Buntings do not share song types with neighbors (Forsythe 1974). We found that some individuals could be individually recognized as did Forsythe (1974) in South Carolina and Georgia. By carefully noting songs, we could relocate specific individuals. We made at least three visits to each song perch to verify the locations of its owner and his neighbors. By using a combination of simultaneous registrations, recognition of individuals when possible, and by corroborating multiple observations of singing

males with the locations of specific song perches, we felt confident that all the song perches used were by different individuals. Song perches of 33 Indigo and 33 Painted buntings were identified.

Habitat features surrounding the song perches were quantified using aerial photographs obtained from the U.S. Geological Survey. Song perch locations were transcribed onto stereoscopic pairs of photographs enlarged to a scale of 1:8000 (1.0 cm = 80 m), and a 229 m diameter circular plot (area = 4.1 ha) was used to define a sampling area around each song perch. To establish the diameter of this sample area the average nearest neighbor distances were first calculated for each species. These distances did not differ between species (Indigo Bunting $\bar{x} \pm SD = 217 \pm 159$ m; Painted Bunting = 240 ± 195 m; *t*-test: $t_{64} = 0.52$, $P > 0.05$). Therefore, we used the overall average nearest neighbor distance of the two species (229 m) as the diameter of the sample area.

Habitat features were identified on the photographs and outlined on transparent overlays. Because the USGS photographs were taken in 1989, the features identified had to be verified by ground surveys. In particular, we verified the locations and sizes of fence rows, isolated trees, stands of trees, and the borders of larger wooded areas. We compensated for changes in the condition of open habitats caused by changes in land use. The data were grouped into three broad categories. Variables that measured vegetation type and successional stage included open habitat, which contained less than 10% coverage by woody vegetation, and wooded habitats, which contained more than 90% coverage by woody vegetation. Wooded habitats were divided into early successional woods, late successional woods, and mature woods. Variables reflecting habitat heterogeneity included the number of isolated trees, the number of stands of trees, the size of the largest open area, the size of the largest stand of trees, the length of edge around the largest stand of trees, and the percent of wooded areas composed of even-aged stands. Physiographic variables were the presence of water, creeks, creek beds, elevation, and type of slope.

Open habitats were areas dominated by grasses, forbs, or both. Early successional vegetation were areas that, on the 1989 photographs, were open, but which in 1996 were colonized by woody vegetation. Stereoscopic imaging allowed vegetation height to be easily estimated. As a result, late successional vegetation could be identified as could the presence and distribution of even-aged stands. The number of stands included all wooded areas bounded by open vegetation and included fencerows and isolated trees. Aquatic habitats consisted of intermittent creeks, permanent creeks, and permanent ponds. Elevation was determined by plotting the song perches onto USGS topographic maps (scale 1:24,000) and interpolating between contour intervals (contour interval was 10 ft). Values were read in ft and subsequently converted to m. Slope was categorized according to whether the

TABLE 1. Area occupied (%) by open habitat, successional woody vegetation, and mature woods for sample areas surrounding the song perches of Indigo and Painted buntings.

Measure	Indigo Bunting Mean \pm SD	Painted Bunting Mean \pm SD	P^a	Adjusted α^b
% Open	48.91 \pm 16.81	49.67 \pm 23.60	0.787	0.050
% Early 2 nd growth	16.12 \pm 9.21	11.70 \pm 10.25	0.012	0.013
% Late 2 nd growth	16.42 \pm 7.56	16.58 \pm 11.42	0.381	0.025
% Mature forest	16.00 \pm 8.10	13.88 \pm 9.37	0.212	0.030

^a Probabilities based on Wilcoxon's Rank-Sum Tests, $n = 33$ for each species.

^b Adjusted values of α needed to reject the null hypothesis based on the sequential Bonferroni method (Rice 1989). Experiment-wise error was set at 5%.

song perch occurred within the top half of a slope, the bottom half of a slope, or on level ground.

The data were analyzed using SAS Release 6.12 on a Windows 95 based computer. The variables were found to be non-normally distributed using Wilk's Statistic (all $P > 0.05$; SAS Institute Inc. 1990); therefore, Wilcoxon's Rank Sum Tests were used for comparisons between species (Pratt and Gibbons 1981). Two variables, types of aquatic habitats present and type of slope, were categorical and were analyzed using χ^2 multiway contingency tables (Model II; Sokal and Rohlf 1995). To test whether the two bunting species were randomly distributed relative to available elevations, the elevation data were stratified into five equal-sized elevation classes. Pearson's χ^2 was then used to test the null hypothesis that the buntings occupied each class with equal frequency.

Because a large number of univariate comparisons were involved in the analyses, the sequential Bonferroni technique was used to adjust the value of α (α_{adj}) necessary to reject the null hypothesis of no difference between species (Rice 1989, Sokal and Rohlf 1995). Based on the discussion by Chandler (1995) we applied this adjustment separately to three families of comparisons that corresponded to the three classes of variables measured; vegetation type, habitat heterogeneity, and physiographic variables. Experimental error was set at 5% for each family of tests (Chandler 1995).

RESULTS

The song perches of both Indigo and Painted buntings were invariably adjacent to edges

between open and wooded habitats (all song perches were in trees). Therefore, all of the sample areas contained some wooded habitat and some open habitat. There was no difference between species with respect to the amount of open habitat surrounding the song perches (Table 1) and, by corollary, there was no difference between species in the amount of wooded habitat surrounding their song perches. Similarly, Indigo and Painted buntings did not differ with regard to the presence or amount of early second growth, late second growth, or mature woods (Table 1). There was considerable variation among the individuals of both species as to which vegetation type was dominant within the sample area around the song perch.

Though the two species did not differ in the amount of each vegetation type found around their song perches, there were marked differences in the spatial patterns of these features (Table 2). Thus, while both species occupied sites that contained similar proportions of wooded habitat, Indigo Buntings were associated with fewer isolated trees and fewer stands of trees (Table 2). As a result, the average size of tree stands and the largest tree stand were larger for Indigo Buntings than

TABLE 2. Vegetation variables in sample areas surrounding the song perches of Indigo and Painted buntings.

Measurement	Indigo Bunting Mean \pm SD	Painted Bunting Mean \pm SD	P^a	Adjusted α^b
Number of isolated trees	2.91 \pm 5.10	4.30 \pm 4.61	0.0155	0.0167
Number of tree stands	5.67 \pm 5.78	8.45 \pm 5.11	0.0030	0.01
Size of tree stands (m ²)	9119 \pm 9032	4040 \pm 6093	0.0047	0.0125
Size of largest open area (m ²)	14,004 \pm 5782	12,331 \pm 5058	0.2637	0.025
Size of largest stand of trees (m ²)	14,706 \pm 7436	8723 \pm 5132	0.0005	0.0071
Length of edge around largest stand of trees (m)	228.7 \pm 54.1	229.5 \pm 54.3	0.6572	0.05

^a Probabilities based on Wilcoxon's Rank-Sum Tests, $n = 33$ for each species.

^b Adjusted values of α needed to reject the null hypothesis based on the sequential Bonferroni method (Rice 1989). Experiment-wise error was set at 5%.

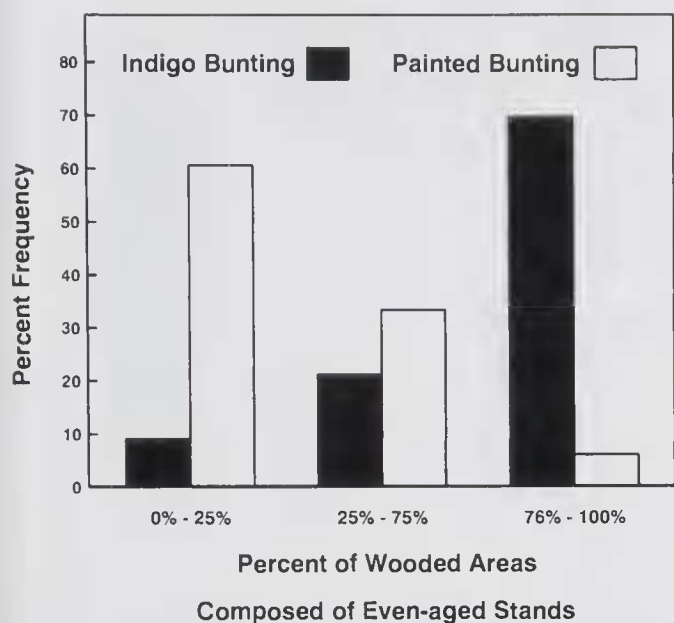


FIG. 1. Presence of even-aged stands of trees surrounding the song perches of Indigo and Painted buntings. Data are expressed in terms of the percentage of stands of trees within the sample areas that were of uniform age.

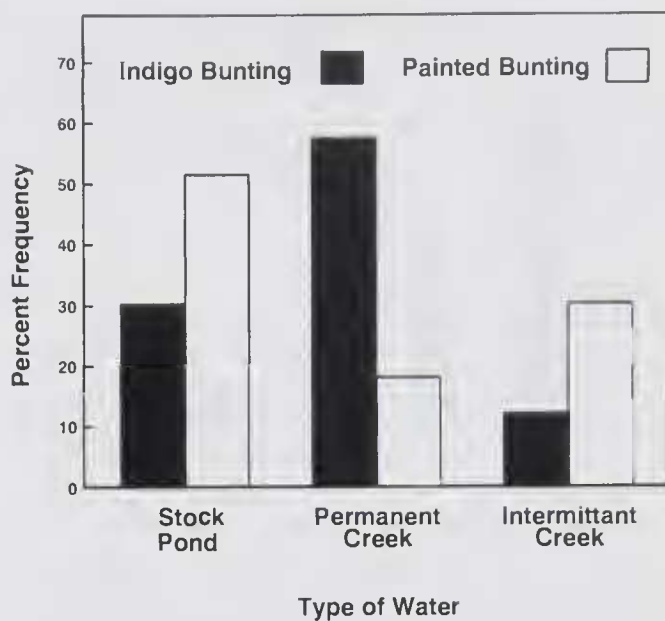


FIG. 2. Types of aquatic habitats found adjacent to the song perches of Indigo and Painted buntings. Permanent creeks always contained water and were found at lower elevations. Intermittant creeks occurred at higher elevations and were often dry.

they were for Painted Buntings (Table 2). However, there was no difference between species relative to the size of the largest open area surrounding their song perches (Table 2).

Given that the largest stand of trees was larger for Indigo Buntings than it was for Painted Buntings, it might be predicted that the edges around these stands should also be longer for Indigo Buntings than for Painted Buntings. Contrary to this expectation, there was no difference between species in the length of edge around the largest wooded area (Table 2). This was because Indigo Bunting song perches frequently occurred on or near linear edges of extensive woodlands. On the other hand, the largest wooded areas associated with Painted Buntings were often irregular clumps of trees or long narrow strips of trees such as those along intermittent streams.

Indigo and Painted buntings also differed relative to the number of even-aged stands of trees surrounding their song perches (Wilcoxon's Rank-Sum Test: $S = 1505.5$, $P = 0.0001$, $\alpha_{adj} = 0.008$; Fig. 1). In this case, the two species exhibited opposing tendencies. For Indigo Buntings, the majority of wooded areas consisted of even-aged stands, whereas for Painted Buntings, the majority of wooded areas were uneven-aged stands (Fig. 1).

Both species tended to be associated with

water. For Indigo Buntings 94% of sample areas contained some aquatic habitat, whereas for Painted Buntings, 82% of sample areas contained some aquatic habitat. These percentages did not differ among species (Contingency table: $\chi^2 = 2.28$, $df = 1$, $P = 0.177$, $\alpha_{adj} = 0.025$). However, the two species differed relative to the type of aquatic habitats present (Contingency table: $\chi^2 = 11.15$, $df = 2$, $P = 0.005$, $\alpha_{adj} = 0.013$; Fig. 2). Indigo Buntings were more often found near permanent creeks than were Painted Buntings.

Indigo Buntings occurred more frequently at lower elevations than at higher elevations (Pearson's χ^2 : $\chi^2 = 22.00$, $df = 4$, $P = 0.001$, $\alpha_{adj} = 0.01$) whereas Painted Buntings showed no tendency to favor any particular elevation (Pearson's χ^2 : $\chi^2 = 2.61$, $df = 4$, $P = 0.626$, $\alpha_{adj} = 0.05$; Fig. 3). As a result, the song perches of Indigo and Painted buntings differed with respect to elevation (Wilcoxon's Rank-Sum Test: $S = 821$, $P = 0.0003$, $\alpha_{adj} = 0.008$; Fig. 3). There were differences between species in the types of slope on which the song perches occurred (Contingency table: $\chi^2 = 10.40$, $df = 2$, $P = 0.006$, $\alpha_{adj} = 0.017$; Fig. 4). Thus, while both species most frequently occupied song perches on level ground, when these perches were located on slopes Painted Buntings were more likely to

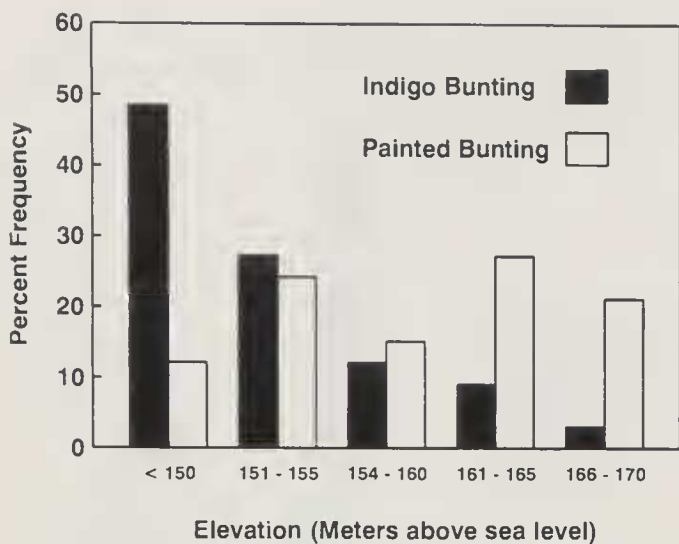


FIG. 3. Surface elevations of Indigo and Painted bunting song perches in meters above mean sea level. The data were stratified into five elevation classes and the bars represent the percent of song perches for each species falling into each elevation class.

occur on upper slopes while Indigo Buntings occurred more frequently on lower slopes (Fig. 4).

DISCUSSION

The Indigo and Painted buntings observed in this study occupied a variety of habitats and showed considerable overlap in habitat use. They did not differ relative to vegetation type, successional stage, or the proportion of open and wooded habitat present. However, there were marked differences with respect to habitat heterogeneity. This latter result indicates that the two species are, to some extent, segregated by habitat. Indigo and Painted buntings do not hold interspecific territories (Forsythe 1974); we never observed agonistic interactions between them, and they sometimes sang in the same trees without interaction. Thus, the habitat differences we observed seem to represent differences in habitat selection, although it remains possible that the species exercise passive avoidance.

Indigo Buntings are known to occupy a variety of habitats. In Iowa, they were found in 12 different habitats, ranging from tilled row crops and herbaceous fencerows to upland and bottomland forests (Best et al. 1995). However, in eastern Kansas, Indigo Buntings were more abundant in young forests than in cropland, old fields, or mature hardwood forests (Zimmerman and Tatschl 1975). In northwestern Arkansas, Indigo Buntings preferred



FIG. 4. Locations of Indigo and Painted bunting song perches relative to surface inclination.

xeric forests and woodland edges over old fields, shrubby fields, or mesic forests (Shugart and James 1973). In Wisconsin, Indigo Buntings favored intermediate successional woodlands over pioneer forests or climax forests (Bond 1957). In Illinois, Indigo Buntings were more frequent in early successional shrub habitats than in late successional shrub habitats, bottomland forests, or mature upland forest (Karr 1968). In our study, Indigo Buntings showed a strong affinity for lower elevations and were most often associated with mesic woods and the uniform successional growth typical of moist bottomlands that have been cleared.

Prior to settlement, Indigo Buntings occupied successional habitats and disturbed areas within the continuous eastern forests of North America (Wells 1958). Consequently, they benefit from disturbances that create openings in wooded areas and settle along the edges of agricultural land (Johnston 1947, Warbach 1958, Gates and Gysel 1978) and forest clearcuts (Strelke and Dickson 1980, Yahner 1987, Wigley and Roberts 1994). The Indigo Buntings we observed were no exception. In the bottomlands where they were most frequent, they occurred along edges created by clearing forests for pastures and hay fields.

Painted Buntings also occupied a variety of habitats, but differed from Indigo Buntings in several ways. The most obvious difference was that, while Indigo Buntings usually occurred in openings in otherwise wooded habitats, Painted Buntings were usually found

where there were clumps of trees in otherwise open habitat. The wooded patches associated with Painted Buntings were of uneven age and had a high ratio of edge to area. This was because these patches were often long and narrow (fencerows and trees along intermittent streams) or irregular clumps. In the latter case, and in contrast to the abrupt edges associated with Indigo Buntings, these edges were more subtle, natural edges.

Our study site lies on the edge of the post oak savanna ecoregion of Texas (Blair 1950), and the habitat favored by Painted Buntings resembled this environment. Similar environments occur to the north and northeast, where Painted Buntings show similar habitat preferences. In Oklahoma this species is most common in open areas dissected by small stands or strips of trees (Parmelee 1959). In Arkansas, Painted Buntings occupy open areas with clumps of small trees (Shugart and James 1973). However, the distribution of the Painted Bunting includes the southeastern pine forests of Texas and Louisiana, and a disjunct population occurs in the Carolinas, Georgia, and northeastern Florida. In southeast Texas, Painted Buntings are more abundant along narrow strips of mature riparian forest than along medium or wide strips of riparian forest (Dickson et al. 1995), a habitat superficially similar to the one we described. However, in South Carolina, Painted Buntings occur at the interface between coastal forests and salt marshes (Lanyon and Thompson 1986) and along rivers in coastal plain forests (Sprunt 1968), habitats unlike those we described. Therefore, our data on Painted Bunting habitat cannot, without further study, be extrapolated across the distribution of this species, especially in the east. Painted Buntings are Neotropical migrants that have shown significant population declines across their range (Sauer et al. 1997). As a result, there is a strong mandate for further studies on the ecology of this species.

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